ISOLATION IN ORGANIC EVOLUTION.

A POSTHUMOUS ESSAY BY THE LATE GEORGE JOHN ROMANES.

THE PRESENT ARTICLE will be devoted to the considera-
tion of what, in my opinion, is one of the most important
principles that are concerned in the process of organic evolution—
namely, Isolation. I say in *my* opinion such is the case, because,
although the importance of isolation is more or less recognised by
every naturalist, I know of only one other who has perceived all
that the principle involves. This naturalist is the Rev. J. Gulick,
and to his essays on the subject I attribute a higher value than to
any other work in the field of Darwinian thought since the date of
Darwin's death.[1] For it is now my matured conviction that a new
point of departure has here been taken in the philosophy of Dar-
winism, and one which opens up new territories for scientific ex-
ploration of an endlessly wide and varied character. Indeed I be-
lieve, with Mr. Gulick, that in the principle of Isolation we have a
principle so fundamental and so universal, that even the great
principle of Natural Selection lies less deep, and pervades a region
of smaller extent. Equalled only in its importance by the two basal
principles of Heredity and Variation, this principle of Isolation
constitutes the third pillar of a tripod on which is reared the whole
superstructure of organic evolution.

By isolation I mean simply the prevention of intercrossing be-
tween a separated section of a species or kind and the rest of that

---

[1] It will be remembered that I regard Weismann's theory of heredity, with all
its deductive consequences, as still *sub judice*.

species or kind.   Whether such a separation be due to geograph-
ical barriers, to migration, or to any other state of matters leading
to exclusive breeding within the separated group, I shall indiffer-
ently employ the term isolation for the purpose of designating what
in all cases is the same result—namely, a prevention of intercross-
ing between A and B, where A is the separated portion and B the
rest of the species or kind.

The importance of isolation as against dissimilar forms has
always been fully appreciated by breeders, fanciers, horticulturists,
etc., who are therefore most careful to prevent their pedigree pro-
ductions from intercrossing with any other stock.   Isolation is in-
deed, as Darwin has observed, "the corner-stone of the breeder's
art."   And similarly with plants and animals in a state of nature:
unless intercrossing with allied (i. e., dissimilar) forms is prevented,
the principle of heredity is bound to work for uniformity, by blend-
ing the dissimilar types in one: only when there is exclusive breed-
ing of similarly modified forms can the principle of heredity work
in the direction of change—i. e., of evolution.

Now, the forms of isolation—or the conditions which may lead
to exclusive breeding—are manifold.   One of the most important,
as well as the most obvious, is geographical isolation ; and no one
questions that this has been an important factor in the process of
evolution, although opinions still vary greatly as to the degree of
its importance in this respect.   At one end of the series we may
place the opinion of Mr. Wallace, who denies that any of what
may be termed the evolutionary effect of geographical isolation is
due to "influence exerted by isolation *per se.*"   This effect, he says,
is to be ascribed exclusively to the fact that a geographically iso-
lated portion of a species must always encounter a change of envi-
ronment, and therefore a new set of conditions necessitating a new
set of adaptations at the hands of natural selection.[1]   At the other
end of the series we must place the opinion of Moritz Wagner, who
many years ago published a masterly essay,[2] the object of which

---

[1] *Darwinism*, p. 150.

[2] *The Darwinian Theory, and the Law of Migration* (Eng. Trans., Stan-
ford, London, 1873.)

was to prove that, in the absence of geographical isolation (including migration), natural selection would be powerless to effect any change of specific type.   For, he argued, the initial variations on which the action of this principle depends would otherwise be inevitably swamped by free intercrossing.   Wagner adduced a large number of interesting facts in support of this opinion; but although he thus succeeded in enforcing the truth that geographical isolation is an important aid to organic evolution, he failed to establish his conclusion that it is an indispensable condition.   Nevertheless, he may have been right—and, as I shall presently show, I believe he was right—in his fundamental premiss, that in the presence of free intercrossing natural selection would be powerless to effect divergent evolution.   Where he went wrong was in not perceiving that geographical isolation is not the only form of isolation.   Had it occurred to him that there may be other forms quite as effectual for the prevention of free intercrossing, his essay could hardly have failed to mark an epoch in the history of Darwinism.   But, on account of this oversight, he really weakened his main contention, namely, that in the presence of free intercrossing natural selection must be powerless to effect divergent evolution.   This main contention I am now about to reargue.   At present, therefore, we have only to observe that Wagner did it much more harm than good by neglecting to perceive that free intercrossing may be prevented in many other ways besides by migration, and by the intervention of geographical barriers.

In order that we may set out with clearer views upon this matter, I will make one or two preliminary remarks on the more general facts of isolation as these are found to occur in nature.

In the first place, it is obvious that isolation admits of degrees : it may be either total or partial ; and, if partial, may occur in numberless grades of efficiency.   This is so manifest that I need not wait to give illustrations.   But now, in the second place, there is another general fact appertaining to isolation which is not so manifest, and a clear appreciation of which is so essential to any adequate consideration of the subject, that I believe the reason why evolutionists have hitherto failed to perceive the full importance of

isolation, is because they have failed to perceive the distinction
which has now to be pointed out. The distinction is, that isolation
may be either discriminate or indiscriminate. If it be discriminate,
the isolation has reference to the resemblance of the separated in-
dividuals to one another; if it be indiscriminate, it has no such
reference. For example, if a shepherd divides a flock of sheep
without regard to their characters, he is isolating one section from
the other indiscriminately; but if he places all the white sheep in
one field, and all the black sheep in another field, he is isolating
one section from the other discriminately. Or, if geological sub-
sidence divides a species into two parts, the isolation will be indis-
criminate; but if the separation be due to one of the sections de-
veloping, for example, a change of instinct determining migration
to another area, or occupation of a different habitat on the same
area, then the isolation will be discriminate, so far as the resem-
blance of instinct is concerned.

With the exception of Mr. Gulick, I cannot find that any
other writer has hitherto stated this supremely important distinc-
tion between isolation as discriminate and indiscriminate. But he
has fully as well as independently stated it, and shown in a mas-
terly way its far-reaching consequences. Indiscriminate isolation
he calls Separate Breeding, while discriminate isolation he calls
Segregate Breeding. For the sake, however, of securing more de-
scriptive terms, I will coin the words Apogamy and Homogamy.
Apogamy, of course, answers to indiscriminate isolation, or sepa-
rate breeding. Homogamy, on the other hand, answers to discrim-
inate isolation, or segregate breeding: only individuals belonging
to the same variety or kind are allowed to propagate. Isolation,
then, is a genus, of which Apogamy and Homogamy are species.[1]

---

[1] I may here most conveniently define the senses in which all the following
terms will be used throughout the present discussion;—*Species* of isolation are, as
above stated, homogamy and apogamy, or isolation as discriminate and indiscrimi-
nate. *Forms* of isolation are modes of isolation, such as the geographical, the
sexual, the instinctive, or any other of the numerous means whereby isolation of
either species may be secured. *Cases* of isolation are the instances in which any
of the forms of isolation may be at work: thus, if a group of n intergenerants be
segregated into five groups, a, b, c, d, e, then, before the segregation there would

Now, in order to appreciate the unsurpassed importance of isolation as one of the three basal principles of organic evolution, let us begin by considering the discriminate species of it, or Homogamy.

To state the case in the most general terms, we may say that if the other two basal principles are given in heredity and variability, the whole theory of organic evolution becomes neither more nor less than a theory of homogamy,—that is, a theory of the causes which lead to discriminate isolation, or the breeding of like with like to the exclusion of unlike. For the more we believe in heredity and variability as basal principles of organic evolution, the stronger must become our persuasion that discriminate breeding leads to divergence of type, while indiscriminate breeding leads to uniformity. This, in fact, is securely based on what we know from the experience supplied by artificial selection, which consists in the intentional mating of like with like to the exclusion of unlike.

The point, then, which in the first instance must be firmly fastened in our minds is this: so long as there is free intercrossing, heredity cancels variability and makes in favor of fixity of type. Only when assisted by some form of discriminate isolation, which determines the exclusive breeding of like with like, can heredity make in favor of change of type, or lead to what we understand by organic evolution.

Now, the forms of discriminate isolation, or homogamy, are very numerous. When, for example, any section of a species adopts somewhat different habits of life, or occupies a somewhat different station in the economy of nature, homogamy arises within that section. There are forms of homogamy on which Darwin has laid great stress, as we shall presently find. Again, when for these or any other reasons a section of a species becomes in any small degree modified as to form or color, if the species happens to be one where any psychological preference in pairing can be exercised— as is very generally the case among the higher animals—exclusive breeding is apt to ensue as a result of such preference; for there is

have been one case of isolation, but after the segregation there would be five such cases.

abundant evidence to show that, both in birds and mammals, sex-
ual selection is usually opposed to the intercrossing of dissimilar
varieties. Once more, in the case of plants, intercrossing of dis-
similar varieties may be prevented by any slight difference in their
seasons of flowering, of topographical stations, or even, in the case
of flowers which depend on insects for their fertilisation, by differ-
ences in the instincts and preferences of their visitors.

But, without at present going into detail with regard to these
different forms of discriminate isolation, there are still two others,
both of which are of much greater importance than any that I have
hitherto named. Indeed, these two forms are of such immeasur-
able importance, that were it not for their virtually ubiquitous
operation, the process of organic evolution could never have be-
gun, nor, having begun, continued.

The first of these two forms is sexual incompatibility—either
partial or absolute—between different taxonomic groups. If all
hares and rabbits, for example, were as fertile with one another as
they are within their own respective species, there can be no doubt
that sooner or later, and on common areas the two types would
fuse into one. And similarly, if the bar of sterility could be thrown
down as between all the species of a genus, or all the genera of a
family, *not otherwise prevented from intercrossing,* in time all such
species, or all such genera, would become blended into a single
type. As a matter of fact, complete fertility, both of first crosses
and of their resulting hybrids, is rare, even as between species of
the same genus; while as between genera of the same family com-
plete fertility does not appear ever to occur; and, of course, the
same applies to all the higher taxonomic divisions. On the other
hand, some degree of infertility is not unusual as between different
varieties of the same species; and, wherever this is the case, it
must clearly aid the further differentiation of those varieties. It
will be my endeavor to show that in this latter connexion sexual
incompatibility must be held to have taken an immensely impor-
tant part in the differentiation of varieties into species. But mean-
while we have only to observe that *wherever* such incompatibility
is concerned it is to be regarded as an isolating agency of the very

first importance. And as it is of a character purely physiological, I have assigned to it the name Physiological Isolation; while for the particular case where this general principle is concerned in the origination of specific types, I have reserved the name Physiological Selection.

The other most important form of discriminate isolation to which I have alluded is Natural Selection. To some evolutionists it has seemed paradoxical thus to regard natural selection as a form of isolation; but a little thought will suffice to show that such is really the most accurate way of regarding it. For, as Mr. Gulick says, "Natural selection is the exclusive breeding of those better adapted to the environment: . . . . it is a process in which the fittest are prevented from crossing with the less fitted, by the exclusion of the less fitted." Therefore it is, strictly and accurately, a mode of isolation, where the isolation has reference to adaptation, and is secured in the most effectual of possible ways,—i. e., by the destruction of all individuals whose intercrossing would interfere with the isolation. Indeed, the very term "natural *selection*" shows that the principle is tacitly understood to be one of isolation, because this name was assigned to the principle by Darwin for the express purpose of marking the analogy that obtains between it and the intentional isolation which is practised by breeders, fanciers, and horticulturists. The only difference between "natural selection" and "artificial selection" consists in this—that under the former process the excluded individuals must necessarily perish, while under the latter they need not do so. But clearly this difference is accidental: it is in no way essential to the process considered as a process of discriminate isolation. For, as far as homogamous breeding is concerned, it can matter nothing whether the exclusion of the dissimilar individuals is effected by separation or by death.

Natural selection, then, is thus unquestionably a form of isolation of the discriminate kind; and therefore, notwithstanding its unique importance in certain respects, considered as a principle of organic evolution it is less fundamental—and also less extensive—than the principle of isolation in general. In other words, it is but

a part of a much larger whole. It is but a particular form of a general principle, which, as just shown, presents many other forms, not only of the discriminate, but likewise of the indiscriminate kind. Or, reverting to the terminology of logic, it is a sub-species of the species Homogamy, which in its turn is but a constituent part of the genus Isolation.

So much then for homogamy, or isolation of the discriminate order. Passing on now to apogamy, or isolation of the indiscriminate kind, we may well be disposed, at first sight, to conclude that this kind of isolation can count for nothing in the process of evolution. For if the fundamental importance of isolation in the production of organic forms be due to its segregation of like with like, does it not follow that any form of isolation which is indiscriminate must fail to supply the very condition on which all the forms of discriminate isolation depend for their efficacy in the causing of organic evolution? Or, to return to our concrete example, is it not self-evident that the farmer who separated his stock into two or more parts indiscriminately, would not effect any more change in his stock than if he had left them all to breed together?

Well, although at first sight this seems self-evident, it is in fact untrue. For, unless the individuals which are indiscriminately isolated happen to be a very large number, sooner or later their progeny will come to differ from that of the parent type, or unisolated portion of the previous stock. And, of course, as soon as this change of type begins, the isolation ceases to be indiscriminate: the previous apogamy has been converted into homogamy, with the usual result of causing a divergence of type. The reason why progeny of an indiscriminately isolated section of an originally uniform stock—e. g., of a species—will eventually deviate from the original type is, to quote Mr. Gulick, as follows[1]:—"No two portions of a species possess exactly the same average character, and, therefore, the initial differences are for ever reacting on the environment and on each other in such a way as to ensure increasing

---

[1] *Divergent Evolution through Cumulative Segregation* (*Zool. Journal, Linn. Soc.*, Vol. XX., pp. 189-274).

divergence as long as the individuals of the two groups are kept from intergenerating." Or, as I stated this principle in my essay on *Physiological Selection*, published but a short time before Mr. Gulick's invaluable contributions to these topics :

> "As a matter of fact, we find that no one individual 'is like another all in all'; which is another way of saying that a specific type may be regarded as the average mean of all its individual variations, any considerable departure from this average being, however, checked by intercrossing. . . . Consequently, if from any cause a section of a species is prevented from intercrossing with the rest of its species, we might expect that new varieties should arise within that section, and that in time these varieties should pass into new species. And this is just what we do find."[1]

The name which I gave to this cause of specific change was Independent Variability, or variability in the absence of overwhelming intercrossing. But it now appears to me that this cause is really identical with that which was previously enunciated by Delbœuf. Again, in his important essay on *The Influence of Isolation*, Weismann concludes, on the basis of a large accumulation of facts, that the constancy of any given specific type "does not arise suddenly, but gradually, and is established by the promiscuous intercrossing of all individuals." From which, he says, it follows, that this constancy must cease so soon as the condition which maintains it ceases —i. e., so soon as intercrossing (Panmixia) between all individuals ceases, or so soon as a portion of a species is isolated from its parent stock. To this principle he assigns the name of Amixia. But Weismann's Amixia differs from my Independent Variability in several important particulars ; and on this account I have designedly abstained from adopting his term. Here it is enough to remark that it answers to the generic term Isolation, without reference to the *kind* of isolation as discriminate or indiscriminate, homogamous or apogamous. On the other hand, my Independent

---

[1] The passage proceeds to show that in view of this consideration we have a strong additional reason for rejecting the *a priori* dogma that all specific characters must necessarily be useful characters. For it is evident that any divergence of specific character which is brought about in this way need not present any utilitarian significance—although, of course, natural selection will ensure that it shall never be deleterious.

Variability is merely a restatement of the so-called "Law of Del-
bœuf," which, in his own words, is as follows :

"One point, however, is definitely attained. It is that the proposition, which
further back we designated paradoxical, is rigorously true. A constant cause of
variation, however insignificant it may be, changes the uniformity [of type] little
by little, aad diversifies it *ad infinitum*. From the homogeneous, left to itself,
only the homogeneous can proceed ; but if there be a slight disturbance ['léger
ferment'] in the homogeneous, the homogeneity will be invaded at a single point,
differentiation will penetrate the whole, and, after a time—it may be an infinite
time—the differentiation will have disintegrated it altogether."

In other words, the "Law," which Delbœuf has formulated on
mathematical grounds, and with express reference to the question
of segregate breeding, proves that, no matter how infinitesimally
small the difference may be between the average qualities of an
isolated section of a species compared with the average qualities of
the rest of that species, if the isolation continues sufficiently long,
differentiation of specific type is necessarily bound to ensue. But,
to make this mathematical law biologically complete, it ought to
be added that the time required for the change of type to super-
vene (supposing apogamy to be the only agent of change) will be
governed by the range of individual variability which the species in
question presents. A highly stable species (such as the Goose)
might require an immensely long time for apogamy alone to pro-
duce any change of type in an isolated portion of the species, while
a highly variable species (such as the Ruff) would rapidly change
in any portion that might be indiscriminately isolated. It was in
order to recognise this additional and very important factor that I
chose the name Independent *Variability* whereby to designate the
diversifying influence of merely indiscriminate isolation, or apog-
amy. Later on Mr. Gulick published his elaborate papers upon
the divergence of type under all kinds of isolation ; and retained
my term Independent, but changed Variability into Generation. I
point this out merely for the sake of remarking that his Indepen-
dent Generation is exactly the same principle as my Independent
Variability, and Delbœuf's Mathematical Law.

Now, while I fully agree with Mons. Giard where he says, in

the introductory lecture of his course on *The Factors of Evolution,*[1] that sufficient attention has not been hitherto given by naturalists to this important factor of organic evolution (apogamy), I think I have shown that among those naturalists who have considered it there is a sufficient amount of agreement. *Per contra,* I have to note the opinion of Mr. Wallace, who steadily maintains the impossibility of any cause other than natural selection (i. e., one of the forms of homogamy) having been concerned in the evolution of species. But at present it is enough to remark that even Professor Ray Lancaster—whose leanings of late years have been to the side of ultra-Darwinism, and who is therefore disposed to agree with Mr. Wallace wherever this is logically possible—even Professor Ray Lankaster observes :

> " Mr. Wallace does not, in my judgment, give sufficient grounds for rejecting the proposition which he indicates as the main point of Mr. Gulick's valuable essay on *Divergent Evolution through Cumulative Segregation.* Mr. Gulick's idea is that . . . . no two portions of a species possess exactly the same average character. and the initial differences will, if the individuals of the two groups are kept from intercrossing, assert themselves continuously by heredity in such a way as to ensure an increasing divergence of the forms belonging to the groups, amounting to what is recognised as specific distinction. Mr. Gulick's idea is simply the recognition of a permanence or persistency in heredity, which, *caeteris paribus,* gives a twist or direction to the variations of the descendants of one individual as compared with the descendants of another."[2]

Now we have seen that "Mr. Gulick's idea," although independently conceived by him, had been several times propounded before ; and it is partly implicated in more than one passage of the *Origin of Species,* where free intercrossing, or the *absence* of isolation, is alluded to as maintaining the *constancy* of a specific type.[3] Moreover, it is still more fully recognised in the last edition of the *Variation of Animals and Plants,* where a paragraph is added for the purpose of sanctioning the principle in the imperfect form that it was stated by Weismann.[4] Nevertheless, to Mr. Gulick belongs the credit, not only of having been the first to conceive (though

---

[1] *Revue Scientifique,* Nov. 23, 1889.   [2] *Nature,* Oct. 10, 1889, p. 368.
[3] *E. g.,* p. 81.   [4] See Chapter xxiii, vol. ii, p. 262. (Edition of 1888.)

the last to publish) the "idea" in question, and of having stated it
with greater fulness than anybody else; but still more of having
verified its importance as a factor of organic evolution.

For, in point of fact, Mr. Gulick was led to his recognition of
the principle in question, not by any deductive reasoning from
general principles, but by his own particular and detailed observa-
tions of the land mollusca of the Sandwich Islands. Here there
are an immense number of varieties belonging to several genera;
but every variety is restricted, not merely to the same island, but
actually to the same valley. Moreover, on tracing this fauna from
valley to valley, it is apparent that a slight variation in the occu-
pants of valley 2 as compared with those of the adjacent valley 1,
becomes more pronounced in the next—valley 3, still more so in 4,
etc., etc. Thus it was possible, as Mr. Gulick says, roughly to es-
timate the amount of divergence between the occupants of any two
given valleys by measuring the number of miles between them.

As already stated, I have myself examined his wonderful col-
lection of shells, together with a topographical map of the district;
and therefore I am in a position to testify to the great value of Mr.
Gulick's work in this connexion, as in that of the utility question
previously considered. The variations, which affect scores of spe-
cies, and themselves eventually run into fully specific distinctions,
are all more or less finely graduated as they pass from one isolated
region to the next; and they have reference to changes of form
and color, which in no one case presents any appearance of utility.
Therefore—and especially in view of the fact that, as far as he
could ascertain, the environment in the different valleys was essen-
tially the same—no one who examines this collection can wonder
that Mr. Gulick attributes the results which he has observed to the
influence of apogamy alone, without any reference to utility or nat-
ural selection.

To this solid array of remarkable facts Mr. Wallace has noth-
ing further to oppose than his customary appeal to the argument
from ignorance, grounded on the usual assumption that no princi-
ple other than natural selection *can* be responsible for even the mi-
nutest changes of form or color. For my own part, I must confess

that I have never been so deeply impressed by the dominating influence of the *a priori* method as I was on reading Mr. Wallace's criticism of Mr. Gulick's paper, after having seen the material on which this paper is founded. To argue that every one of some twenty contiguous valleys in the area of the same small island must necessarily present such differences of environment that all the shells in each are differently modified thereby, while in no one out of the hundreds of cases of modification in minute respects of form and color can any human being suggest an adaptive reason therefor,—to argue thus is merely to affirm an intrinsically improbable dogma in the presence of a great and consistent array of opposing facts.

I have laid special stress on this particular case of the Sandwich Islands' mollusca, because the fifteen years of labor which Mr. Gulick has devoted to their exhaustive working out have yielded results more complete and suggestive than any which so far have been forthcoming with regard to the effects of isolation in divergent evolution. But, if space permitted, it would be easy to present abundance of additional facts from other sources, all bearing to the same conclusion,—namely, that as a matter of direct observation, no less than of general reasoning, any unprejudiced mind will concede to the principle of indiscriminate isolation an important share in the origination of organic types. For as indiscriminate isolation is thus seen sooner or later to become discriminate, and as we have already seen that discriminate isolation is a necessary condition to all or any modification, we can only conclude that isolation in both its kinds takes rank with heredity and variability as one of the three basal principles of organic evolution.

Having got thus far in the way of generalities, we must next observe sundry further matters of comparative detail.

1. In any case of indiscriminate isolation, or apogamy, the larger the bulk of the isolated section the more nearly must its average qualities resemble those of its parent stock ; and, therefore, the less divergence of character will ensue in a given time from this cause alone. For instance, if one-fourth of a large species were to be separated from the other three-fourths (say, by sub-

sidence causing a discontinuity of area), it would continue the spe-
cific characters unchanged for an indefinitely long time, so far as
the influence of such an indiscriminate isolation is concerned. But,
on the other hand, if only half a dozen individuals were to be thus
separated from the rest of their species, a comparatively short time
would be needed for their descendants to undergo some varietal
modification at the hands of apogamy. For, in this case, the
chances would be infinitely against the average characters of the
original half-dozen individuals exactly coinciding with those of all
the rest of their species.

2. In any case of homogamy, however, it is immaterial what
proportional number of individuals are isolated in the first instance.
For the isolation is here discriminate, or effected by the initial dif-
ference of the average qualities themselves—a difference, therefore,
which presupposes divergence as having already commenced, and
equally bound to proceed whether the number of intergenerants be
large or small.

It may here be remarked that, in his essay on the *Influence of
Isolation*, Professor Weismann fails to distinguish between the two
kinds of isolation. This essay deals only with one of the many
different forms of isolation—the geographical—and is therefore
throughout concerned with a consideration of diversity as arising
from apogamy alone. But in dealing with this side of the matter
Weismann anticipated both Gulick and myself in pointing out the
law of inverse proportion, which I have stated in the preceding
paragraph in what appears to me its strictly accurate form.

3. Segregate Breeding, or homogamy, which arises under any
of the many forms of discriminate isolation, must always tend to
be *cumulative*. For, again to quote Mr. Gulick, who has constituted
this fact the most prominent as it is the most original feature of his
essay, " In the first place, every new form of Segregation[1] that now
appears depends on, and is superimposed upon, forms of Segrega-
tion that have been previously induced ; for when Negative Segre-
gation arises [i. e., isolation due to mutual sterility], and the va-

---

[1] This term may here be taken as equivalent to isolation.

rieties of a species become less and less fertile with one another, the complete infertility that has existed between them and some other species does not disappear, nor does the Positive Segregation cease [i. e., any other form of isolation previously existing]. . . . In the second place, whenever Segregation is directly produced by some quality of the organism, variations that possess the endowment in a superior degree will have a larger share in producing the segregated forms of the next generation, and accordingly the segregative endowment of the next generation will be greater than that of the present generation ; and so with each successive generation the segregation will become increasingly complete." And to this it may be added, in the third place, that where the segregation (isolation) is due to the external conditions of life under which the organism is placed, or where it is due to natural selection simultaneously operating in divergent lines of evolution, the same remarks apply. Hence it follows that discriminate isolation is, in all its forms, cumulative.

4. The next point to be noted is, that the cumulative divergence of type thus induced can take place only in as many different lines as there are different *cases* of isolation. This is a point which Mr. Gulick has not expressly noticed ; but it is one that ought to be clearly recognised. Seeing that isolation secures the breeding of similar forms by exclusion (immediate or eventual) of those which are dissimilar, and that only in as far as it does this can it be a factor in organic evolution, it follows that the resulting segregation, even though cumulative, can only lead to divergence of organic types in as many directions as there are cases of isolation. For any one group of intergenerants only *serial* transformation is possible, even though the transformation be cumulative through successive generations in the single line of change. But there is always a probability that during the course of such *serial transformation in time*, some other case of isolation may supervene, so as to divide the previously isolated group of intergenerants into two or more further isolated groups. Then, of course, opportunity will be furnished for *divergent transformation in space*—and this in as many different lines as there are now different homogamous groups.

That this must be so is further evident, if we reflect that the evolutionary power of isolation depends, not only on the *preventing* of intercrossing between the isolated portion of a species and the rest of that species, but also upon the *permitting* of intercrossing between all individuals of the isolated portion, whereby the peculiar average of qualities which they as a whole present may be allowed to assert itself in their progeny—or, if the isolation has been from the first discriminate, whereby the resulting homogamy may thus be allowed to assert itself. Hence any one case of either species of isolation, discriminate or indiscriminate, can only give rise to what Mr. Gulick has aptly called "monotypic evolution," or a chain-like series of types arising successively in time, as distinguished from what he has called "polytypic evolution," or an arborescent multiplication of types arising simultaneously in space.

For example, let us again take the geographical form of isolation. Where a single small intergenerant group of individuals is separated from the rest of its species—say, on an oceanic island— *monotypic* evolution may take place through a continuous and cumulative course of independent variation in a single line of change : all the *individuals* composing any one given generation will closely resemble one another, although the *type* may be progressively altering through a long series of generations. But if the original species had had two small colonies separated from itself (one on each of two different islands, so giving rise to two cases of isolation), then *polytypic* evolution would have ensued to the extent of there having been two different lines of evolution going on simultaneously (one upon each of the two islands concerned). Similarly, of course, if there had been three or four such colonies, there would have been three or four divergent lines of evolution, and so on.

5. In the *cases* of isolation just supposed there is only one *form* of isolation ; and it is thus shown that under one form of isolation there may be as many lines of divergence as there are separate cases of such isolation. But now suppose that there are two or more forms of isolation—for instance, that on the same oceanic island the original colony has begun to segregate into secondary groups under the influence of natural selection, sexual selection,

physiological selection, or any of the other forms of isolation—then there will be as many lines of divergent evolution going on at the same time (and here on the same area) as there are forms of isolation affecting the oceanic colony. And this because each of the *forms* of isolation has given rise to a different *case* of isolation.

Now, inasmuch as different forms of isolation, when thus superadded one to another, constitute different cases of isolation, we may lay down the following general law as applying to all the forms of isolation,—namely, *The number of possible directions in which divergent evolution can occur, is never greater than, though it may be equal to, the number of cases of efficient isolation— or the number of efficiently separated groups of intergenerants.*

6. We have now to consider with some care the particular and highly important form of isolation that is presented by natural selection. For while this form of isolation resembles all the other forms of the discriminate kind in that it secures homogamy, there are two points in which it differs from all of them, and one point in which it differs from most of them.

Natural selection differs from *all* the other known forms of isolation (whether discriminate or indiscriminate) in that it has exclusive reference to *adaptations* on the one hand, and, on the other hand, necessitates not only the elimination, but the destruction of the excluded individuals. Again, natural selection differs from *most* of the other forms of isolation in that, unless assisted by some other form, it can never lead to polytypic, but only to monotypic evolution. The first two points of difference are here immaterial; but the last is one of the highest importance, as we shall immediately perceive.

In nearly all the other forms of isolation, polytypic or divergent evolution may arise under the influence of that form alone, or without the necessary co-operation of any other form. This we have already seen, for example, in regard to geographical isolation, under which there may be as many different lines of transmutation going on simultaneously as there are different cases of isolation,— say, in so many different oceanic islands. Again, in regard to physiological isolation the same remark obviously applies; for it is

evident that even upon the same geographical area there may be as many different lines of transmutation going on simultaneously as there are cases of this form of isolation. The bar of mutual sterility, whenever and wherever it occurs, must always render polytypic evolution possible. And so it is with almost all the other forms of isolation : that is to say, one *form* does not necessarily require the assistance of another *form* in order to create an additional *case* of isolation. But it is a peculiarity of natural selection, considered as a form of isolation, that it does necessarily require the assistance of some other form before it can give rise to an additional case of isolation ; and therefore before it can give rise to any *divergence* of character in ramifying lines, as distinguished from *transformation* of characters in a single line. Or, in other words, natural selection, when acting alone, can never induce polytypic evolution, but only monotypic.

That this important conclusion is a necessary deduction from the theory of natural selection itself, a very few words will be enough to show. For, according to the theory, survival of the fittest is a form of isolation which acts through utility, by *destroying* all the individuals whom it fails to isolate. Hence it follows that survival of the fittest is a form of isolation which, if acting alone, cannot *possibly* effect divergent evolution. For, in the first place, there is nothing in this form of isolation to ensure that the fitter individuals should fail to interbreed with the less fit which are able to survive ; and, in the second place, in all cases where the less fit are not sufficiently fit to be suffered to breed, they are exterminated —i. e., not permitted to form a distinct variety of their own. If it be said that survival of the fittest may develop simultaneously two or more lines of *useful* change, the answer is that it can only do this if each of the developing varieties is isolated from the others by some *additional form* of isolation ; for, if not, there can be no commencement of utilitarian *divergence*, since whatever number of utilitarian changes may be in course of simultaneous development, they must in this case be all blended together in a single line of specific transmutation. Nay, even if specific divergence has actually been commenced by natural selection when associated with some other form

of homogamy, if the latter should afterwards be withdrawn, natural selection would then be unable to maintain even so much divergence of character as may already have been attained : free intercrossing between the two collateral, and no longer isolated branches, would ensure their eventual blending into a common stock. Therefore, I repeat, natural selection, when acting alone, can never induce polytypic evolution, but only monotypic.

Now I regret to say that here, for the first and only time throughout the whole course of my treatment of these subjects, I find myself in seeming opposition to the views of Darwin. For it was the decidedly expressed opinion of Darwin that natural selection *is* competent to effect polytypic, or divergent, evolution. Nevertheless, I believe that the opposition is to a large extent only apparent, or due merely to the fact that Darwin did not explicitly state certain considerations which throughout his discussion on "divergence of character" are seemingly implied. But, be this as it may, I have not even appeared to desert his leadership on a matter of such high importance without having duly considered the question in all its bearings, and to the utmost limit of my ability, Moreover, about two years after the publication of my first paper[1] upon the subject, Mr. Gulick followed, at somewhat greater length, in the same line of dissent. Like all the rest of his work, this is so severely logical in statement, as well as profoundly thought out in substance, that I do not see how it is possible for any one to read impartially what he has written, and then continue to hold that natural selection, if unassisted by any other form of isolation, can possibly effect divergence of character—or polytypic as distinguished from monotypic evolution.[2]

I may here quote from Mr. Gulick's paper three propositions, serving to state three large and general bodies of observable fact, which severally and collectively go to verify, with an overwhelming mass of evidence, the conclusion previously reached on grounds of general reasoning.

---

[1] *Zool. Journal Lin. Soc.*, Vol. XIX. pp. 337–411.

[2] *Ibid.*, Vol. XX. pp. 202–211.

"The facts of geographical distribution seem to me to justify the following statements :

"1. A species exposed to different conditions in the different parts of the area over which it is distributed, is not represented by divergent forms when free interbreeding exists between the inhabitants of the different districts. In other words, Diversity of Natural Selection without Separation does not produce divergent evolution.

"2. We find many cases in which areas, corresponding in the character of the environment, but separated from each other by important barriers, are the homes of divergent forms of the same or allied species.

"3. In cases where the separation has been long continued, and the external conditions are the most diverse in points that involve diversity of adaptation, there we find the most decided divergences in the organic forms. That is, where Separation and Divergent Selection have long acted, the results are found to be the greatest.

"The 1st and 3rd of these propositions will probably be disputed by few, if by any. The proof of the 2nd is found wherever a set of closely allied organisms is so distributed over territory that each species and variety occupies its own narrow district, within which it is shut by barriers that restrain its distribution, while each species of the environing types is distributed over the whole territory. The distribution of terrestrial molluscs on the Sandwich Islands presents a great body of facts of this kind."